PACKARD (A. S.) Jr.

AUTHOR'S EDITION.

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CHAPTER XI.

THE BRAIN OF THE LOCUST.

In order to appreciate the habits, migratory, reproductive, &c., of the locust, and to learn something of its general intelligence as an insect and as compared with other insects, it is necessary for us to study with a good deal of care the organ of the locust's *mind*, *i. e.*, its nervous system, comprising its nervous centers and the nerves arising from them. The present chapter will be devoted to a study of the brain.

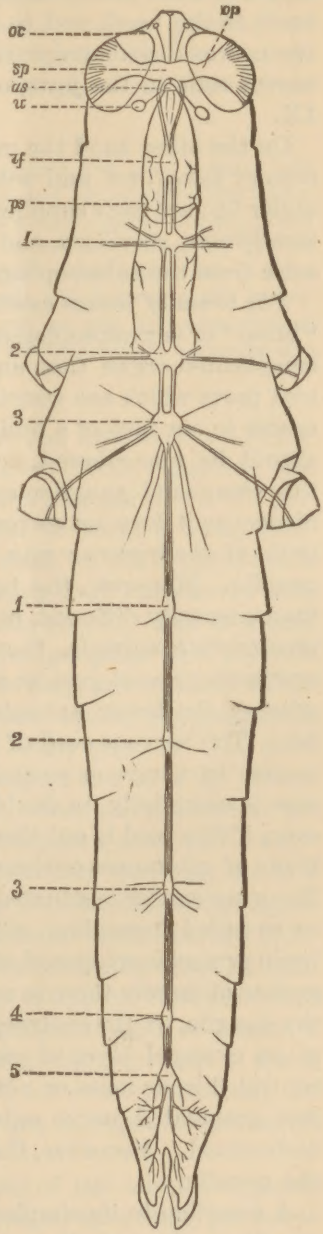

FIG. 9.

The nervous system in general.—The nervous system of the locust has been described in a general way in the First Annual Report of the Commission (p. 264, Figs. 14, 15). It consists of a series of nerve centers or *ganglia*, connected by nervous cords called *commissures*. There are ten of these ganglia in the locust, *i. e.*, two in the head, the first and largest of which is called the "*brain*"; there are three ganglia in the thorax, and five in the hind-body or abdomen. The brain is situated in the upper part of the head, resting upon the gullet or œsophagus, whence its true name *supraœsophageal ganglion.* (Plate IX, Fig. 1.) The succeeding nerve-center is situated in the lower part of the head, behind the mouth and under the œsophagus, hence it is called the *subœsophageal ganglion.* (Plate IX, Fig. 5.) The supraœsophageal ganglion is larger than the succeeding ones, and is compressed from before and behind, its height being much greater than its length, while the other ganglia are more or less lens-shaped and flattened vertically, being broader than thick. The brain really is a double ganglion, being composed of two hemispheres, each hemisphere being a single ganglion or nerve-center; all the succeeding ganglia are also double ganglia; but for convenience we will call the "brain" and each of the succeeding nerve-centers a *ganglion.* Each side of the brain contracts, and then swells out into a rounded portion next to the eye, called the *optic ganglion.* From this optic ganglion the optic

fibers proceed to the facets of the eye. The optic ganglion connects with the brain by the large optic nerve. There are, then, two *optic nerves*, besides three slender nerves (*ocellar nerves*) sent to each of the three *ocelli* or simple eyes; moreover, a nerve is sent to each of the antennæ and are hence called the *antennal* nerves. The relations of the brain to the head, and to the succeeding ganglion, and the origins of the nerves distributed to the eyes, antennæ and ocelli, as well as of the nerves sent to the jaws, etc., are clearly seen in the figures on Plate IX.

On the other hand the mouth parts, *i. e.*, the jaws (*mandibles*) and accessory jaws (first and second *maxillæ*, the latter called the *labium* or under lip) are each supplied by a pair of nerves, called, respectively, the *mandibular*, *maxillary*, and *labial* nerves. These three pairs of nerves arise from the subœsophageal ganglion. (See Pl. IX, Fig. 2.)

The brain of insects as distinguished from the brain of vertebrates.—The "brain" or supraœsophageal ganglion is, as we shall see, a much more complicated organ than any of the succeeding ganglia, having important parts which are wanting in all the others, hence it is *par excellence* nearer to our idea of a brain than any of the other nervous centers. It should be remembered, however, that the word "brain" is applied to this compound ganglion simply by courtesy and as a matter of convenience, as it does not correspond to the brain of a vertebrate animal, the brain of the horse or man being composed of several distinct pairs of ganglia. Moreover, the brain and nervous cord of the fish or man is fundamentally different, or not homologous with that of the lower or invertebrate animals, though the nervous system of the insects and crustacea present greater analogies to that of the vertebrates than any other of the lower animals, with the exception, perhaps, of the cuttle-fish. The nervous cord of the insect consists of a chain of ganglia connected by nerves or commissures, while the spinal cord of the fish or man is essentially "a double and fused series of nerve-centers." Moreover, if this cord is cut through, a section shows that it consists of two kinds of substances or tissues, called the "gray" and "white" substance. The gray matter is situated in the center, and consists largely of nerve or so-called "ganglion cells," while the external white matter of the brain or cord is composed of a mass of nerve fibers. Now, in the nervous system of insects there is nothing to compare with these substances, but the ganglia, on the contrary, as we shall see farther on, consist primarily of an external layer of ganglion cells, whose fibers pass in to form a central fibrous mass or net-work, the meshes of which are filled with a fine granulated nerve substance, the nature of which is not clearly understood. Moreover, the entire brain of an insect is white, as are all the ganglia.

A ganglion in its simplest form is a little rounded mass, or nodule, of ganglion cells, with fibers leading from them; such cells are represented by Fig. 3*a*, on Plate XI. Now when the fibers lead in from the sensitive

hairs on the crust of the insect, or from the antennæ, or the eyes or ears, and end in separate masses or lobes, which are modified ganglia, such ganglia are regarded as "sensory ganglia," and the nerves leading in from them are called ingoing or "afferent nerves," while the ganglia which give rise to the outgoing or "efferent" nerves, *i. e.*, those going to the muscles of the wings, legs, &c., are called "motor ganglia," as stated by Bastian, in his popular and excellent work "The Brain as an Organ of Mind." As to the term ganglion we quote as follows from Bastian:

> Two or more sensory ganglia, or two or more motor ganglia, may grow together into a single mass; or, what is equally common, a sensory and its corresponding motor ganglion, or two or more pairs of these, may fuse into a single larger nodule, which may be called a "nerve-center." The term ganglia is, however, commonly applied to any round, ovoid nodule containing nerve-cells, whatever its size or degree of internal complexity. Many ganglia in the lower animals, which are typically deserving of the name as regards mere form and separateness, are also, by reason of their compound nature, true nerve-centers. The two terms are, therefore, to a considerable extent, interchangeable.

Referring the reader to Bastian's book, or to the text-books on physiology by Huxley, Foster, or Dalton, for information regarding the structure and physiology of the nervous system in general, we will proceed to describe that of the locust. It should be borne in mind, however, that the subœsophageal ganglion, or "brain," of the insect is much more complex than any other ganglion, consisting more exclusively both of sensory as well as motor ganglia and their nerves. But it should also be borne in mind that the subœsophageal ganglion also receives nerves of special sense, situated possibly on the palpi and possibly on the tongue, at least the latter is the case with the bee; hence, this ganglion is probably complex, consisting of sensory and motor ganglia. The third thoracic ganglion is also, without doubt, a complex one, as in the locusts the auditory nerves pass into it from the ears, which are situated at the base of the abdomen. But in the green grasshoppers, such as the katydids and their allies, whose ears are situated in their fore-legs, the first thoracic ganglion is a complex one. In the cockroach and in the *Leptis* (Chrysopila), a common fly, the caudal appendages bear what are probably olfactory organs, and as these parts are undoubtedly supplied from the last abdominal ganglion, this is probably composed of sensory and motor ganglia; so that we have in the ganglionated cord of insects a series of brains, as it were, running from head to tail, and thus in a still stronger sense than in vertebrates the entire nervous system, and not the brain alone, is the organ of the *mind*, or psychological endowment, of the insect.

We will now proceed to examine the brain of the adult *Caloptenus spretus*, and compare it with that of other insects; then study its development in the embryo, and finally examine the changes it undergoes in

the larva and pupal stages before attaining the fully developed structure of the adult locust.

THE BRAIN OF THE ADULT LOCUST.

The method of examination employed by us has been to cut the brain into a number of thin sections by means of the microtome, previously hardening the tissues in alcohol. The labor of cutting these sections has been performed by Mr. Norman N. Mason, of Providence, R. I., who has brought to his work an unusual degree of skill and care in preparing such delicate sections. In all these sections the brain was not previously removed from the head, but the entire head was cut through, having previously been hardened in absolute alcohol for twenty-four hours or more, and then soaked in gum arabic for one or two or more days. The objects were then embedded in a preparation of paraffine and sweet-oil and wax, or, in some cases, in soap and oil. After the sections were cut they were stained with picrocarmine, or partially stained with osmic acid, and then treated with picrocarmine. Finally the slices were mounted in glycerine jelly for study under the microscope.

The sections were in most cases *frontal* ones, namely, cut transversely from the front of the head or brain backwards, while a few were longitudinal or *vertical* ones, viz, cut parallel to the median line of the body. They were either $\frac{1}{500}$ or $\frac{1}{1000}$ of an inch in thickness.

It should be observed that the brain is divided by a furrow into two halves or hemispheres; these are deepest above and below, and the upper and lower portions may be called, respectively, the *frontal* and *posterior* furrow.

The brain is mostly surrounded by a thin delicate membrane, the neurilemma, also called by Krieger the *perineurium;* it is formed of very dense fibrous connective tissue.

Histological elements of the brain.—The brain is histologically or structurally divided into two kinds of tissue or cellular elements.

I. An outer, slightly darker, usually pale grayish white portion is made up of "cortical cells," or "ganglion cells." (Pl. XI, Fig. 3, *a*, *b*, *c*, *d*.) This portion is stained red by carmine, the ganglion cells composing it readily taking the stain; when thus stained by carmine, the nucleus of the cells is rendered quite distinct, but the cell wall is also distinct; when stained by hæmatoxylin the large nuclei are remarkably distinct, but the cell walls are not well brought out; when stained by osmic acid these cells are not so clearly shown as by a picrocarmine or carmine stain, and the nucleus is less distinct than when treated by the two other stains mentioned.

This outer loose cellular envelope of the brain consists of large and small ganglion cells. Where the tissue consists of small ganglion cells, it is naturally from the denser arrangement of the smaller cells, which are packed closer together, rather darker than in those regions where the tissue consists of the more loosely disposed, large ganglion cells.

A. The large ganglion cells (Pl. XI, Figs. 3, 3 *a*, 3 *b*, 3 *c*, 3 *d*, 3 *e*) are oval, and send off usually a single nerve fiber; they have a thin fibrous cell wall, and the contents are finely granular. The nucleus is very large, often one-half the diameter of the entire cell, and is composed of large round refractive granules, usually concealing the nucleolus (the granules are much larger and fewer in number and the nucleolus is less distinct than in the brain of Limulus, the king crab). These large ganglion cells are most abundant and largest on each side of the upper furrow, and in front of the "central body," also at the bottom of the lower furrow, and along the exterior of the optic and antennal lobes, and along the commissural lobes.

B. The small ganglion cells apparently differ chiefly in size from the large ones, and are most numerous in the front swelling of each hemisphere; they surround and fill the calices of the mushroom bodies, and they extend along each optic nerve and form a large proportion of each optic ganglion, especially the layer next to the retina of the eye, though they are replaced by large ganglion cells at the junction of the fibrous part of the optic nerve with the dilated granular portion. The brain is surrounded more or less completely by the connective tissue cells belonging to the mesoderm or middle germ layer, and which are sometimes liable to be confounded with the ganglion cells, as they stain the same tint with carmine. It should be borne in mind that the nervous system, ganglia and nerves, originate from the tegumental or exodermal layer.

II. The medullary or inner part of the brain consists of matter which remains white or unstained after the preparation has remained thoroughly exposed to the action of the carmine. It consists of minute granules and interlacing fibers. The latter often forms a fine irregular net-work inclosing masses of finely granulated nerve matter.

In the antennal and commissural lobes is a third kind of matter, in addition to the granular and fibrous substances, which forms irregularly rounded masses, cream-colored in picro-carmine preparations, and which stain dark with osmic acid. This is called by Dietl "*marksubstanz*," and is described by Newton as "a peculiar arrangement of nervous matter, which appears sometimes as fine fibrillæ, with an axial arrangement, sometimes as a very fine net-work of different thicknesses, and sometimes as thin lamellæ, or altogether homogeneous. Under all these forms this third group of textures is characterized by turning very dark under the influence of osmic acid, whilst the other elements are only turned brown."

It is to be noticed that this central unstained portion contains few, if any, ganglion cells, and it is most probable that the fibers of which it is composed originate from the cortical ganglion cells. At one or two points at Fig. 3, Pl. XI, I have seen the fibers passing in from ganglion cells towards the middle of the brain. In the horseshoe crab (Limulus), owing to the simple structure of the brain, it is evident that the optic

and ocellar nerves and posterior commissures originate from the large ganglion cells which in this animal are situated in or near the center of the brain. In the last abdominal ganglion also the fibers arising from the peripheral ganglion cells can very plainly be seen passing in towards the center of the ganglion and mingling with the fibers forming it. Hence in all probability the fibrous mass of the central part of the brain mostly originates from the peripheral or cortical ganglion cells.

To briefly describe the brain of the locust, it is a modified ganglion, but structurally entirely different from and far more complicated than the other ganglia of the nervous system. It possesses a "central body," and in each hemisphere a "mushroom body," optic lobe, and optic ganglion, and olfactory lobe, with their connecting and commissural nerve fibers, not found in the other ganglia. In the succeeding ganglia the lobes are in general motor; the fibers composing the œsophageal commissures, and which arise from the œsophageal commissural lobes, extend not only to the subœsophageal ganglion, but pass along through the succeeding ganglia to the last pair of abdominal nerve centers.[326] Since, then, there is a direct continuity in the fibers forming the two main longitudinal commissures of the nervous cord, and which originate in the brain, it seems to follow that the movements of the body are in large part directed or co-ordinated by the brain.[327] Still, however, a second brain, so to speak, is found in the third thoracic ganglion of the locust, which receives the auditory nerves from the ears situated in the base of the abdomen; or in the first thoracic ganglion of the green grasshoppers (katydids, &c.), whose ears are in their fore legs; while even the last abdominal ganglion in the cockroach and mole cricket is, so to speak, a secondary brain, since it receives sensory nerves from the caudal stylets which are provided with sense organs.

Description of the sections of the brain.—We will now describe the sections upon which the subsequent account of the brain is founded. The sections, unless otherwise stated, are *frontal*, *i. e.*, cut transversely across

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[326] We have seen that the two great longitudinal commissures pass directly from the brain into and then pass backward from the subœsophageal ganglion, but beyond that point have not traced their course, as it is generally supposed that they extend uninterruptedly to the last abdominal ganglia. This has indeed been shown to be the case by Michels in his admirable treatise on the nervous system of a beetle (Oryctes) in Siebold and Kölliker's Zeitschrift für wissen. Zoologie, Band 34, Heft. 4, 1880. Michels states that each commissure is formed of three parallel bundles of elementary nerve fibers, which pass continuously from one end of the ventral or nervous cord to the other. "The commissures take their origin neither out of a central "punct substanz (or marksubstanz), nor from the peripheral ganglion cells of the several ganglia, but are mere continuations of the longitudinal fibers which decrease posteriorly in thickness, and extend anteriorly through the commissures forming the œsophageal ring to the brain."

[327] The following extract from Newton's paper shows, however, that the infra or subœsophageal ganglion, according to Faivre, has the power of co-ordinating the movements of the body; still it seems to us that the brain may be primarily concerned in the exercise of this power, as the nerves from the subœsophageal ganglion supply only the mouth parts. "The physiological experiments of Faivre in 1857 (Ann. J. Sci. Nat., tom. viii, p. 245), upon the brain of Dytiscus in relation to locomotion, are of very considerable interest, showing, as they appear to do, that the power of co-ordinating the movements of the body is lodged in the infra-œsophageal ganglion. And such being the case, both the upper and lower pairs of ganglia ought to be regarded as forming parts of the insect's brain." Quart. Jour. Micr. Sc., 1879, p. 342.

the face from before backwards; in cutting thus through the head, twelve sections were made before the front part of the brain was touched, the thirteenth grazing the front of the brain. Section 14 passed through the anterior part of both *calices*, but did not touch the stalk of the *mushroom body* (these terms will be explained farther on). It passed through the central region of each hemisphere, including the front part of the *trabeculæ* or base of the stalk of the mushroom body. The section passed through the commissural lobes, the lower third being composed of ganglion cells, but the substance of the commissure itself is filled with the ball-like masses of "marksubstanz." The commissures to the subœsophageal ganglion were not touched, and do not appear in the section, since they arise from the back of the brain.

In section 15 no additional organs are exposed. In section 16 (Pl. X, Fig. 1) the trabeculæ are seen, when magnified 225 diameters, to be composed of ascending fibers, which form the base or origin of the double stalk of the mushroom body.

Section 17 (Pl. X, Fig. 2) is the most important of all the sections, as the entire mushroom body and the central body are cut through, together with the antennal lobes, and the commissural lobes, and also the origin of the optic nerves.

In section 18 (Pl. X, Fig. 4) the double nature of the stalk of the mushroom body is seen; the optic lobes are now well marked, and the razor grazed the back of the commissural lobes, as well as the inner side of the optic ganglion. The section passed behind the trabeculæ and the base of the stalk and through the back of the central body. The calices are each seen to be so furrowed and uneven as to appear in the section as two separate portions. Two important nerves (Pl. X, Fig. 4, *p. a. n.*) are seen to arise from the commissural lobes, and to pass upwards, ending on each side of the upper furrow, near the origin of what we think are possibly the ocellar nerves (*o. c. n.?*).

Section 19 (Pl. XI, Fig. 1) passed through the back of the brain (compare Fig 4. of the same plate, which represents a vertical or longitudinal section of the brain), through the œsophageal commissures, and the back edge of the calices, while the antennal lobes and a part of the optic lobes are well seen in the section. A transverse commissural nerve (*t c n*) connects the two antennal lobes, and the commissural nerves are seen to cross at the bottom of the furrow.

Section 20 (Pl. XI, Fig. 2), which passes through the extreme back of the brain, shows in this plane four transverse bundles of nerve fibers connecting the two hemispheres, *i. e.*, the inferior (*inf. n.*), two median (m. n.) and, a superior nerve (*sup. n.*). In this section the relations of the optic ganglion and eye to the brain are clearly seen, the optic ganglion being situated in the posterior region of the brain. It will also be seen that the two hemispheres are at this point only connected anteriorly.

In sections 22, 23, and 24 the brain nearly disappeared, and only the

optic ganglia were cut through by the microtome, affording instructive sections of the three lenticular masses of white unstained granulo-fibrous substance surrounded by ganglion cells.

INTERNAL TOPOGRAPHY OF THE BRAIN.

Disregarding the envelope of cortical ganglionic cells, though they are evidently of primary importance in the physiology of the insect's brain, we will now describe the internal topography of the brain. It consists primarily of an irregular net-work of nerve-fibers, inclosing masses of granulated nerve matter. This mass is divided into a number of separate areas or lobes, of which the "central body" (*corpus centrale* of Flögel and Newton) is single and situated between or in the median line of the two hemispheres. There is also a primitive superior and inferior central region, better shown, however, in the brain of the embryo and larval locust than in the adult. Besides these areas are the rounded masses or "lobes," *i. e.*, the optic, antennal, or olfactory and commissural lobes; the optic nerves arising from the optic lobes, the antennal nerves from the antennal lobes, and the commissures surrounding the œsophagus and connecting the brain with the subœsophageal ganglion; these arise from the commissural lobes. Finally a "mushroom body" is situated in the upper and central part of each hemisphere.

The central body.—This is the only single or unpaired organ in the brain. It is best seen in section 17 (Pl. X, Fig. 2), which also passes through the optic and antennal lobes and the trabeculæ and mushroom bodies. This singular organ is apparently present in all winged insects, though differing somewhat in structure in different insects. It is, as seen in Pl. X, Fig. 2, situated in the same plane as the peduncle and in the same plane as the center of the entire mushroom body, and rests upon the inner sides of the trabeculæ. Section 16 does not pass through it, though the next section, which is $\frac{1}{500}$ inch thick, passes through its middle. Section 18 (Fig. 4) passes through its back, while the next section does not include any part of it; hence its antero-posterior diameter is slightly over $\frac{1}{500}$ of an inch. It is about twice as broad as high, and thus is a small body, though from the universality of its occurrence in winged insects, it may be one of considerable importance.

It is surrounded by a dense net-work of fibers containing a few small ganglionic cells, the fibres in front continuous with those near the bottom of the frontal median furrow and connecting the two optic lobes. Posteriorly the fibers apparently are not continuous with those of the trabeculæ; hence the central body appears to be quite isolated from the rest of the brain. Its substance, when magnified 400 diameters, appears to be a white granular matter like the adjoining parts of the brain. It is divided into two parts, the superior and inferior, the former part constituting the larger part of the body. The inferior portion is separated by fibers from the superior; it contains numerous nucleated spherical cells situated either irregularly or perhaps primarily (see Pl. XIV, Fig. 3,

of the pupa), in two rows when fewer in number than in the adult. The superior and larger division of the central body contains the series of what we may call *unicellular bodies*, sixteen in a series. The lower series are spherical or slightly elongated, and rest in the fibrous partition or septum, forming the floor of the superior division of the central body. The upper row of bodies are cylindrical, and about three or four times as long as thick. They are separated by thin fibrous septa. Pl. XIV, Fig. 2, represents the central body enlarged 225 diameters. When we examine the central body in an earlier stage, *i. e.*, the second pupal (Pl. XIV, Fig. 3), we see that the body is covered above by a stratum of nucleated ganglion cells continuous with those next to the bottom of the upper furrow; and that the fibrous septum between the upper and lower division also contains small cells. These cells disappear in the adult, and evidently give rise to the fibers which take their place. It will also be seen that the "unicellular bodies" are shorter, more cell-like, than in the adult; hence they seem to be modified ganglion cells, which have at an early date lost their nucleus and nucleolus. My observations on the central body of the locust agree in the main with those of Newton (compare his Fig. 9). His drawings are not especially clear and definite, but the differences appear to be unimportant. There are perhaps two (16 instead of "12 or 14") more cellular bodies in the locust than in the cockroach. Unfortunately my sections of the brain of the cockroach do not show the central body. Dietl states that the central body is a "median commissural system." This description we would accept in a modified sense. We have shown that the unicellular bodies and the cells beneath them were once like the ganglion cells, but that they have lost their nuclei and nucleoli; hence the functions of the central body must be unlike that of an ordinary commissural lobe. Flögel states that the number of "sections," or what I call unicellular bodies, is eight; we have counted sixteen. Both Flögel and Newton appear to regard these bodies as simply spaces or sections between fibrous partitions; but it would appear that these sections are really modified cells, and that the fibrous septa, are possibly the cell-walls, somewhat modified.

The mushroom bodies.—These curious organs have attracted a good deal of attention from writers on the brain of insects. Dujardin, in 1850, first drew attention to them. His memoir we have not at hand to refer to, but as stated by Newton [328]—

Dujardin pointed out that in some insects there were to be seen upon the upper part of the brain certain convoluted portions which he compared to the convolutions of the mammalian brain, and, inasmuch as they seemed to be more developed in those insects which are remarkable for their intelligence, such as ants, bees, wasps, &c., he seemed to think the intelligence of insects stood in direct relationship to the development of these bodies. The form of these structures is described by the same author as being, when fully developed, as in the bee, like a pair of disks upon each side,

[328] On the Brain of the Cockroach. By E. T. Newton. Quart. Journ. Microscopical Science, July, 1879, II, pp. 341, 342.

each disk being folded together and bent downwards before and behind, its border being thickened and the inner portion radiated. By very careful dissection he found these bodies to be connected on each side with a short pedicle, which bifurcates below to end in two tubercles. One of these tubercles is directed towards the middle line, and approaches but does not touch the corresponding process of the opposite side. The second tubercle is directed forwards, and is in close relation to the front wall of the head, being only covered by the pia mater [neurilemma]. These convoluted bodies and the stalks upon which they are mounted are compared by Dajardin to certain kinds of mushrooms, and this idea has been retained by more recent writers on the subject.

The form of the mushroom body is much more complicated in the bee or ant than in insects of other orders. In the cockroach and in other Orthoptera, notably the locust, the four divisions of the calices are united into two; while the structure of the calyx in the cockroach is quite different from that of the locust. Mr. Newton, in his description, notwithstanding Dujardin's statement, appears to practically limit the term "mushroom body" to the cap or calyx on the end of the stalk. In the following description we apply the term "mushroom body" to the entire structure, including the base or trabecula, the double stalk, and the cap or calyx.

So far as we have been able to observe, the double stalk of the mushroom body rests on a rounded mass of granulo-fibrous nerve matter; this rounded mass or base of the column is called the *trabecula* (Pl. X, Fig. 2, *trab.*). The two trabeculæ (one in each hemisphere) are much more widely separated (in my sections) than in the cockroach or in those insects studied by Flögel; the space between them being filled by a loose cellular mass containing small nucleated cells. The thickness of each trabecula is greater than that of the double stalk. Section 14 passes through the outer or anterior edge of the trabecula, and also through the calices at some distance from the edge. Section 18 (Fig. 4) does not include it, though showing well the mushroom body, with the exception of the base of the double stalk. It follows that the thickness of the trabecula is about $\frac{3}{500}$ of an inch.

The substance of the trabecula is seen to be minutely fibrous under a power of 725 diameters, with masses of granules among the fibers which are much finer than in the optic or antennal lobes. At the point passed through by section 17 the trabeculæ appear to have no connection with the stalk, but the latter appear to stop abruptly just before reaching it, the envelope of ganglionic cells and fibers surrounding the trabeculæ being interposed between the base of the stalk and the trabecula. (This does not preclude the fact that the stalk does not arise from the trabecula, though there are no signs of it in this section; for it clearly appears to thus arise in the drawings and descriptions of Dietl, Flögel, and Newton).

The structure of the trabeculæ in the locust, judging from our sections, appears to be more complex than would be inferred from the observations of the other observers just mentioned. Section 17 (Pl. X, Fig. 2, *trab.*) passes through the middle of each of these bodies, and it then ap-

pears that there are four bundles of nerve-fibers passing out of each body. A bundle of transverse nerve-fibers (Fig. 2 *t. c. n.* and Fig. 3) passes along under the central body, directly through the middle of the trabeculæ, and anastomoses with the fibrous envelope of each trabecula. In front of this transverse intra-trabecular nerve is a small short ascending bundle of fibers (Fig. 3, *a. t. n.*) which passes next to the pedicel, but does not apparently form a part of it, but anastomoses with the fibers on each side of the central body. Below, the fibres pass downward and outward to apparently connect with the fibrous envelope of the trabecula. Another short bundle passes out from the trabecula obliquely towards the central body and anastomoses with the fibrous envelope of the central body.

Below, but in the same plane, is another transverse bundle of fibers (Fig. 3, *l. t. n.*), which is slightly curved and on the left side its fibers are distinctly seen to enter the trabecula. This lower intratrabecular nerve, as we may call it, connects with three vertical short nerves arising from near the edge of the lower furrow between the hemispheres of the brain. Of these, the central one (*centr. n.*) is in the median line of the brain, and the lateral ones (*lat. n.*) are on each side. There would thus seem to be a direct double nervous communication between the two trabeculæ, and with the fibers surrounding the central body, and hence with the rest of the brain. This seems to be opposed to the statement of Newton that the trabeculæ, and the mushroom bodies in general, have no nervous connection with the rest of the brain. This section also clearly indicates the origin of the optic nerve, which passes *behind* the stalk of the mushroom body, and also the relation of the fibers of the stalk to the calices, as they appear to penetrate far into the interior of the body of each calyx.

The double stalk (*cauliculus* and *peduncle*).—These names are applied to the larger and smaller divisions of the stalk of the "mushroom body." They are represented in the eighteenth section (Fig. 4) where the outer part of the stalk (*cauliculus*) supports the outer calyx, and the inner slenderer column of fibers supports or ends in the inner division of the calyx. These two bundles of fibers are somewhat curved, but as they do not appear in sections 16 and 19, must be less than $\frac{2}{500}$ of an inch thick. Their fibers are seen to penetrate deeply into the base of the calices, and thus to directly communicate with the fine granular substance of the calices.

The calices.—The cups of the mushroom bodies in the locust differ decidedly in form from those of the cockroach, and this part of the mushroom body is more variable in form in the different orders of insects than any of the other parts of the brain. It is nearly obsolete, or, as Flögel states, "not more than rudimentary" in hemipterous insects (notably *Syromastes*), and is less completely developed in many smaller moths, beetles, and flies, as well as Neuroptera (*Æschna*), according to Flögel, than in the larger moths, in the Orthoptera, and especially in the

Hymenoptera, where it is well developed. We have been unable to find it as yet in the brain of myriopods or of the spider. In the locust each body is more or less rounded and rudely saucer-like rather than cup-like, with the rim very thick; the hollow of the cup, if it be hollow, is small in proportion to the thickness of the saucer-like cup. The diameter of a calyx is about $\frac{7}{500}$. The anterior edge reaches to the front edge of each hemisphere of the brain, but does not extend to the back part of the brain. The relations in a vertical, *i. e.*, longitudinal section of the mushroom body to the rest of the brain are seen in (Pl. X, Fig. 8 *a*). It thus appears that the double stalk is situated near the center of the brain, and that the cap projects far forward, but posteriorly does not extend behind the antennal lobes or the commissures. In section 18 (Fig. 4) the calices are seen to be double, the outer (*o. cal.*) attached to the cauliculus (*cau.*) and the inner arising from the peduncle. Fig. 8 *a* gives an idea of the two calices and their mode of attachment to the stalk. The peduncle (if we interpret that division of the stalk aright) subdivides, sending a thick bundle of fibers to each calyx, ending abruptly in the hollow of the calyx. The substance of the calices is finely granular, with some coarse granules, and apparently short scattered irregular fibers. The structure of the calices of the locust appears to be more homogeneous than that of the cockroach, judging by our sections of the latter. Owing to different treatment by reagents the dark masses described by Newton as existing in the cockroach were not so clearly shown in my sections ($\frac{1}{1000}$ inch thick) as in those made by Mr. Newton. The substance of the calices when examined under a power of 725 diameters is much the same both in the cockroach and the locust, the dark bodies not appearing in either. The form of the calices is very different in the cockroach, the calices being truly cup-like, the disk being deeply folded, and the edges of each cup being thin compared with those of the locust.

The optic lobes.—As seen in section 19 (Pl. XI, Fig. 1 *op. l.*) these bodies are larger than the antennal lobes, and consist of numerous irregular small bundles of fibers besides those composing the optic nerve, the interspaces being filled with fine granular nerve substance. The optic nerve is much larger at the outer edge of the lobe before passing into the optic ganglion, the fibers still being immersed in the finely granular nervous substance.

The optic ganglion.—This is situated at the back of the brain, and is a large rounded mass of white fine granular nervous matter, enveloped in very numerous but small ganglion cells, which stain dark red by carmine, the granular matter remaining unstained by the picrocarmine. The granular or white portion is subdivided into three rudely lens-shaped masses (see Pl. XV, Fig. 1), the one nearest the eye being much the largest. The structure of the optic ganglion is substantially as described by Newton, as seen in his description and our preparations. A farther description is reserved for our account of the eye, which we hope to give in the next report.

The antennal or olfactory lobes.—Section 19. (Pl. XI, Fig. 1., *ant. l.*) These are smaller than the optic lobes, though in section 19 they appear larger. They give rise to the antennal nerve, and as the locust carries its ears at the base of the abdomen, the auditory nerves entering the third thoracic ganglion, reasoning by exclusion the antennæ in Orthoptera must be organs of smell, and the lobes and nerves to the antennæ are consequently olfactory. This is the opinion of some recent writers, notably Hauser.[329] The lobes are, as described by the other observers, filled with ball-like yellowish masses, which stain dark by osmic acid, much as in the commissural lobes. Nerve fibers are seen in section 19 to pass from one antennal lobe to the other in the rear of the central body and of the trabeculæ, while other nerve fibers are seen to pass into the optic lobes and the commissural lobes. This system of intralobal nerves demonstrates that there is a nervous intercommunication between these cerebral lobes and the ganglionic chain of the entire body.

The commissural lobes.—From these large bodies proceed the two great longitudinal commissural nerves, forming the connecting threads of the nervous cord, and which extend from the brain to the last abdominal ganglion, passing through the intermediate nerve centers. The lobes are filled with ball-like masses, of the same general appearance as in the antennal lobes, but more distinct and numerous.

Comparison of the brain of the locust with that of other insects.—Newton rightly regards the cockroach's brain as a generalized form of brain, which may serve as a standard of comparison. The cockroach is geologically one of the oldest of insects; its external and internal structure is on a generalized plan, and the brain conforms to this order of things. Our knowledge of the cockroach's brain is derived from the photographs and account of Flögel, and Newton's excellent descriptions and figures, supplemented by two sets of sections made for us by Mr. Mason, but which, unfortunately, are quite defective as regards the trabeculæ and stalk of the mushroom body. The shape of the calices of the cockroach, as already stated, is very different from that of these bodies in the locust, and indeed from any other insect, the cup being very deep and the sides thin; but the intimate structure seems nearly the same in the two insects.

In the cockroach the antennal and commissural lobes are of much looser texture, with large and numerous ball-like masses (*ballensubstanz*); these are, when magnified 400 diameters, not only larger, but more distinct from the rest of the nervous matter of the lobe than in the locust. When magnified as mentioned, the ball-like masses appear to be simple masses of finely granular nervous matter, with darker granules, much like the rest of the granular portions of the brain, but with coarser granular masses than in the substance of the optic lobes. These ball-like masses are surrounded by a loose net-work of anastomosing nerve fibers continuous with those of the antennal nerve, and with scattered

[329] Physiologische und histiologische Untersuchungen über das Geruchsorgan der Insekten. Siebold und Kölliker's Zeitschrift für Wissen. Zoologie, Bd. 34, Heft. 3.

nucleated cells, which become very numerous in the antennal nerve. The nerve fibers are stained reddish by the picrocarmine.

Turning now to other orthopterous insects, Flögel mentions Acrydium, but states that he had no serviceable preparations, and after describing the brain of Forficula, the ear-wig, says: "As I observe in Acrydium, the cells and fibers in this animal are especially large, and these objects invite further investigation." Flögel's photograph and description of the brain of Forficula, a representative of an aberrant family of Orthoptera, and Dietl's beautiful figures and descriptions of the brain of the mole-cricket (*Gryllotalpa vulgaris*) and the cricket (*Acheta campestris*) show that the orthopterous brain, judging from these representative forms, is constructed on a common type, the most variable part being the calices of the mushroom body.

From these facts we should judge that, on the whole, the locusts were as highly endowed intellectually as any other insects, with the exception of the ants, bees, or wasps, *i. e.*, the social species; while in a number of insects the brain is less developed than in the locust. It would thus appear that, as in the vertebrates, there are different grades of brain-development, considerable extremes existing in the same sub-class of insects, as in the same sub-class of mammals.

The brain of the bee and ant, as shown by Dujardin and demonstrated by Dietl and Flögel, is constructed on a higher, more complicated type than in the other winged insects, owing to the much greater complexity of the folds of the calices or folded disk-like bodies capping the double stalk of this organ.

STRUCTURE OF THE BRAIN IN THE EMBRYO LOCUST.

Much light may be thrown upon the structure of different parts of the adult brain if we can trace their origin in the embryo, or in the larval and pupal conditions. Hence, we have, with what material we could obtain, made a series of sections of the embryo and different stages of the larva and pupa, with some results of considerable interest and importance. No one has yet examined the brain of the embryo insect. The only observer who has studied the brain of the larva, as compared with the adult, has been Flögel. Speaking of the cockroach, he says:

> Of especial interest would be an investigation of the development of the separate parts of the brain. The difficulty of making preparations of small heads has been such that no particular results have been reached. Still, I can say this much, that in small creatures 7–8^{mm} in length all the parts are present, only of a finer and more delicate structure than in the large adult 25^{mm} in length.

He says that in the Hymenoptera he has discovered much concerning the development of the parts of the brain; that in bee larvæ the calices are present, though very small and with thin walls. The peduncle and trabecula have reached their ultimate proportions more nearly than the cauliculus, which is still very thin. In the larval ants the central body and entire mushroom bodies are present, though an early larval

stage shows, in place of the calices, four symmetrically situated balls of much smaller size; the central body was very flat, and the other parts were wanting. In the pupa all the parts had attained their definite shape. It appears from his observations that the calices are the last to be developed.

He then gives the results of his examination of the brain of caterpillars, as compared with that of the adult sphinx moth. In a caterpillar examined near the time of pupation, the central body is very much undeveloped, forming a small linear transverse body (Querleiste), while the different parts of the mushroom body are indicated. In smaller caterpillars it is scarcely possible to work out the development of the brain. In that of *Pontia brassicæ* the mushroom body and central body were undeveloped, while in that of an Euprepia larva the double stalk of the mushroom body was developed as well as roundish calyx masses. But in a Noctuid larva the entire mushroom body, including well-developed trabeculæ and a very flat central body, was present.

The brain of the mature pupæ of Lepidoptera, for example *Saturnia carpini*, contains all the portions of the adult brain, and in the same relative proportions. But a brain of *Sphinx ligustri*, in a considerably younger stage of development, did not differ much from the brain of the larva.

We offer the following observations on the brain of the embryo locust, shortly before hatching, with much diffidence, as we are liable to be corrected by future observations in the same directions. The embryos were taken from the egg-shell, hardened in the usual manner, and then cut by Mr. Mason, the sections being frontal, the entire insect being embedded in a mixture of paraffine, wax, and oil.

In the youngest stage (which we will call stage A) observed, the body and appendages were formed and the eyes with their facets, the pigment mass coloring the cornea pale reddish.

At this stage, as seen in section 7 (Pl. XII, Fig. 1), the antennal and optic lobes of the brain are indicated, but the central body and mushroom bodies are not yet differentiated. In a plane lying in front of the optic and antennal lobes, the brain is divided in each hemisphere into two regions or lobes, *i. e.*, an upper (Figs. 1 and 8, *up l*) and lower cerebral lobe (*low l*). From these embryonic cerebral lobes are eventually developed the central body and the two mushroom bodies. The stratum of cortical ganglionic cells is, at this period, quite distinct from the paler unstained granular brain matter. Pl. XII, Fig. 1 *a*, represents the structure of the ganglionic cell-portion, which gradually passes into the central white brain substance, which is composed of fine granules or nuclei alone, and which do not apparently differ from the granules scattered among the ganglion cells. It is to be observed that there are no fibers among the granules. It thus appears that the brain of insects, like the other ganglia, originally consists of a paler portion formed of fine clear granules (nuclei?), enveloped by a thick irregular layer of nucleated cells, containing fine granules outside of the nucleus.

As the fibers of the adult brain are evidently secondary products, it would appear that they must be transformed granules or nuclei, and not in all cases, at least, the fibers thrown off from the ganglion cells, although at this time the ganglion cells have no fibers, the fibers of those seen in the adult brain being also secondary growths. It may be that the white inner granulo-fibrous matter of the adult brain is (1) made up of modified granules, which in some cases remain such, and in others form fibers, and (2) of fibers sent in from the cortical ganglion cells.

Comparison of the brain at this stage with the first thoracic ganglion.—If we compare at this stage of development of the nervous system the brain with one of the ganglia of the trunk, we shall obtain a fair idea of the primitive difference between the brain and one of the ordinary ganglia (Pl. XIII, Fig. 5). By a glance at the figures of the two it will be seen that the organization of the thoracic ganglion is essentially simple. It is divided into two portions or regions. The central granular region is enveloped by a thick stratum of cortical ganglion cells. The whole ganglion in section is rudely hour-glass-shaped and much smaller than the brain. There is no differentiation into distinct lobes as in the brain. The formation of the brain, as is well known by embryologists, is one of the earliest steps in the development of the nervous system, the entire system being at an early date in the life of the embryo set apart from the epidermis or integument, the latter with the nervous system originating from the ectoderm or outer germ-layer.

Second embryonic stage, B (Pl. XII, Figs. 2–9).—In embryos more advanced, and just ready to hatch, the eyes being now dark red, the central body is formed, but our sections do not show any traces of a mushroom body. The sections are frontal, and we will describe them in order. The fifth section is through the head and front part of the eyes, but does not graze the brain itself. Fig. 2 shows the structure of the interior of the head, being filled with connective tissue cells not distinguishable from the ganglion cells.

Section 6 (Fig. 3) passes through the outer portion of the optic and antennal lobes, now clearly differentiated.

In section 7 the cerebral lobes are seen, and in section 8 are larger, as are the optic lobes, while the antennal lobes are somewhat reduced in size. Section 10 passes through the cerebral lobes and also grazes the optic lobes, passing through the optic ganglion.

Section 11 (Fig. 8) shows the central body, separated from the upper cerebral lobes by a thin layer of loose ganglionic cells. The relation of the central body to the upper and lower cerebral lobes is well shown in this section.

Plate XIII, Fig. 4, shows the relation of these and their structure greatly enlarged. Through the granular substance of the lobes are sparsely scattered ganglionic cells.

Section 12 passes through the lower cerebral lobes and the upper left

cerebral lobe and the optic ganglion. The œsophagus is situated beneath the cleft under the lower cerebral lobes. The next section (13) passes behind the brain, not touching it. These sections are $\frac{1}{500}$ inch thick.

Structure of the subœsophageal ganglion (Pl. XII, Fig. 10).—In its form this nerve center is more like the brain than the first thoracic ganglion. The figure is drawn from the youngest embryo observed. The ganglion seen in section is very much larger and quite different in shape from the thoracic ganglia. It expands above the lower fissure between the two sides, being very deep and narrow, while the superior furrow is broad and shallow. The internal paler portion (when magnified 400 diameters) is seen to consist of granules. The stratum of outer cells (the future ganglion cells) is thickest on the outside of the upper part of the ganglion, and at the base of each hemisphere.

The brain of the freshly-hatched larva of C. spretus.—In the larva but a few hours after hatching, the brain, so far as I can learn from four sections, does not essentially differ from that of the embryo just before hatching, as the interval is apparently too short for a decided change to take place. It is evident that by the end of the first larval stage the brain attains the development seen in the third larval state of the two-banded species.

For illustrations of the different larval and pupal stages of development of the locust the reader is referred to the first Report of the Commission (Plates I, II, III).

Third larval stage of Caloptenus bivittatus (Pl. XIII, Fig. 1–3).—In the third larval condition of another species, the common *Caloptenus bivittatus* of our gardens, the different parts of the brain have attained nearly the same structure and proportions as in the adult. Pl. XIII, Fig. 1, represents a section passing through the front of the brain, and also the lateral ocelli and the right eye. The ganglion cells surrounding and filling the calices are smaller and more crowded than elsewhere. The mushroom bodies are now formed, though the trabeculæ are not to be seen in our section, but the entire double stalk and calices are very clearly seen. The fibers from the stalk are observed to extend along the inner edge of each calyx and to suddenly stop just beyond the middle. The granular calices contain slight irregularities and sinuous lines, as shown in Fig. 2, *i. cal.*, *o ca.*, but to what these appearances are due it is difficult to say; there are also a few scattered large granules. As the section passes through the front of the brain, where the hemispheres are separated by the frontal furrow, the lobes are not well marked, but the substance is made up of irregular intercrossing bundles of fibers, with the interspaces filled with granulated matter. In Fig. 3 the regular saucer-like form of the calyx is well shown. Fig. 2 is an enlarged view of the right side of Fig. 1, and at this stage large important bundles of fibers are seen passing into the optic, antennal, and commissural lobes.

First pupal stage of Caloptenus spretus.—My sections are too imperfect to describe, but the form of the brain is closely like that of the next stage.

Second or last pupal stage of Caloptenus spretus.—A number (14) of very successful sections made by Mr. Mason from one head give an excellent opportunity for studying the head of the locust in this stage, just before becoming fledged (see first Report, Pl. I, Fig. 5). Of these sections, Nos. 8 and 9 pass through the calices and œsophageal lobes, but do not reach the central body. Section 10 (Fig. 1 of Pl. XIV) passes through the central body, which is $\frac{1}{500}$ of an inch in thickness, the section itself being of the same thickness. In the optic ganglion the section passes through the front of it, but two lenticular masses appear. The trabeculæ are as in the adult, and the superior and inferior intra-trabecular nerves are clearly seen to pass into the center of each trabecula just as in the adult. On the left side the origin of the cauliculus and peduncle is clearly seen, under a power of 225 and of 400 diameters, the relation of parts being exactly as in the adult (see Pl. X, Fig. 3). The base of the two divisions of the double stalk arise suddenly, as if inserted into or resting simply upon, rather than arising from, the trabeculæ; the bases of the cauliculus and peduncle being in the same line with the base of the center of the upper division of the central body. It appears as if a few nerve fibers passed under the base of the stalk between it and the trabecula; at any rate, I have been unable to observe either in the pupa or larva or adult, among a number of preparations, any continuity between the trabeculæ and the double stalk.

In this section the curving of the double stalk backwards and the passage in front of this double column is to be clearly seen, and is just as we have described it from similar sections of the adult brain (Fig. 3 of Pl. X). The ball like masses in the œsophageal commissures are as distinctly shown as in the adult.

Section 11 passes behind the central body, not showing it nor the basal part of the double stalk of the mushroom body. This section, and those behind it, show well the structure of the optic ganglion. In section 11 the three lenticular bodies clearly appear.

The main, and almost the only, difference between the second pupa and the adult appears to be in the degree of development of the central body. In the second pupa (Pl. XIV, Fig. 3) it is rather more elementary than in the adult, the upper and lower series of unicellular bodies being a little shorter and rounder, nearer their primitive condition, and the septa between them are plainly fibrous. Their contents are as finely granular as the adjoining parts of the body.

Section 11 is instructive as showing a bundle of directly ascending and obliquely ascending fibers from the back part of the trabecula, of which a portion is contained in the section. Two large bundles enter the commissural lobes, one from above and one from the inner side under the central body, the bundle from above passing down into the lobe from around the upper side of the trabecula. From this fact we should infer

that there is a partial nervous communication between the trabeculæ and the commissural lobes. The fibers enveloping the trabecula above are more numerous, the mass of fibers much thicker than in section 10, showing that what we supposed to be fibers separating the stalk from the trabecula appear to be really such.

A broad bundle of fibers is also seen on the right side, passing down from the upper side inside of the upper end of the peduncle, down outside and back of the central body, and to enter the commissural lobe on its inner side, terminating at the point where the ascending fibers to the upper side of the trabecula originate. There is thus a direct communication between the upper part of the brain and the œsophageal commissure in the lower part. It appears, also, that three large nerves or bundles of fibers enter each commissural lobe from above.

At the under side of the commissural lobes the cortical ganglion cells (some of them very large) appear to send their fibers into others to build up the mass of fibers enveloping the lobe. Flögel states that the opinion that the ganglionic cells in winged insects are in direct relation through the fibers with the organs of the body are unfortunately provisionally contradicted by his observations. But here (seen in a portion of the commissural lobe not represented in Fig. 3 of Pl. XI), as in one or two other places, we think we have seen fibers from the cortical ganglion cells passing into and aiding in building up the nerves. Such a relation is very plain in the brain of the horseshoe-crab, *Limulus polyphemus*.

LIST OF WORKS ON THE INTERNAL STRUCTURE OF THE BRAIN OF CRUSTACEA AND INSECTS.

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MICHELS. Beschreibung des nervensystems von Oryctes nasicornis in Larven, Pup-

pen, und Käferzustande. Von H. Michels. Zeitschrift für wissens. Zoologie. Bd. xxxiv, p. 641–702. Pl. 33–36. 1880.

PACKARD. On the internal structure of the Brain of Limulus Polyphemus. By A. S. Packard, jr. American Naturalist, June, 1880, p. 444–448.

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KRIEGER. Ueber das Centralnervensystem des Flusskrebses. Von K. R. Krieger, Zeitschrift für wissenschaft. Zoologie. Bd. xxxiii, Jan. 23, 1880, p. 527. Plates.

EXPLANATIONS OF PLATES IX–XV.

Plate ix was drawn by Mr. E. Burgess from his own dissections of *Caloptenus femur-rubrum*, a species so closely allied to the Rocky Mountain locust that the same drawings will answer for both species. Plates x–xv were drawn by A. S. Packard, jr., with the camera lucida, nearly all the details as well as the outlines being drawn with the aid of the camera.

LETTERING OF THE FIGURES ON PLATES IX–XV.

centr. b., central body.
trab., trabecula.
cau., cauliculus.
ped., peduncle.
o. cal., outer calyx.
i. cal., inner calyx.
op. l., optic lobe.
op. n., optic nerve.
ant. l., antennal lobe.
ant. n., antennal nerve.
œ. com. l., œsophageal commissural lobe.
œ. com. n., œsophageal commissural nerve.
l. g. c., large ganglion cells.
s. g. c., small ganglion cells.
opt. gang., optic ganglion.
t. n., transverse nerve.
u. intr. n., upper intratrabecular nerve.
l. intr. n., lower intratrabecular nerve.
lat. n., lateral nerve.
centr. n., central nerve.
obl. tr. n., oblique trabecular nerve.
a. t. n., ascending trabecular nerve.
m. n., two median commissural nerves.
sup. n., superior commissural nerve.
inf. n., inferior commissural nerve.
tr., trachea.
up. l., upper cerebral lobe of embryo.
low. l., lower cerebral lobe of embryo.
gang. c., ganglion cells.
gran., granules of the central nervous matter.
œs., œsophagus.
int., integument.
o. n., ocellar nerve.
n. c., ventral nervous cord.
n. c. l., nucleolus.

PLATE IX.

Fig. 1. Front view of the brain of *Caloptenus femur-rubrum*: *opt. gang.*, optic ganglion; *oc.*, ocelli and nerves leading to them from the two hemispheres, each ocellar nerve arising from the region containing the calices; *m. oc.*, median ocellar nerve; *opt. l.*, optic lobe sending off the optic nerve to the optic ganglion; *ant. l.*, antennal or olfactory lobe; *ant. n.*, antennal nerve; *f. g.*, frontal ganglion of sympathetic nerve; *lbr. n.*, nerve to labrum; *x*, cross-nerve or commissure between the two hemispheres; *œ. c.*, œsophageal commissure to subœsophageal ganglion.

2. Side view of the brain and subœsophageal ganglion (lettering of brain as in fig. 1): *s. g.*, stomatogastric or sympathetic nerve; *a. s. g.*, anterior, and *p. s. g.*, posterior, sympathetic ganglia; *g.* 2, subœsophageal ganglion; *md.*, nerve to mandible; *mx.*, maxillary nerve; *ln.*, labial nerve; *n. ?*, unknown nerve, perhaps salivary?

3. Interior view of the right half of the head, showing the brain in its natural position: *an.*, antenna; *cl.*, clypeus; *lbr.*, labrum; *m.*, mouth cavity; *md.*, mandible; *t.*, tongue; *œ.*, œsophagus; *c*, crop; *en.*, right half of the endocranium or X-shaped bone, through the anterior angle of which the œsophagus passes, while the great mandibular muscles play in the lateral angles. The moon-shaped edge is that made by the knife passing through the center of the X.

4. View of brain from above (letters as before).

5. Subœsophageal ganglion from above: *t. c.*, commissure to the succeeding thoracic ganglion; other letters as before.

Fig. 3 is enlarged eight times; all the rest twenty-five times.

NOTE.—The figures on this plate were drawn from original dissections by Mr. Edward Burgess.

E. Burgess del. Meisel lith Boston

PLATE X.

Fig. 1.—Frontal section 16, through the front of the brain of adult *Caloptenus spretus*; × ⅛ inch objective, A. eye-piece.

Fig. 2.—Section 17, showing the central body (*centr. b.*) and mushroom body, optic and antennal lobes, and commissural lobes; × ⅛ A.

Fig. 3.—Enlarged view of the trabecula and its nerves, of the mushroom body, its calices and stalk, and the origin of the optic nerves; for lettering see schedule. × ⅛ A., 225 diameters.

Fig. 4.—Section 18, passing through the back of the central body, showing the double nature of the stalk of the mushroom body, and passing through the back of the commissural lobes and behind the trabecula and the base of the stalk; × ⅛ A. Are *oc. n.*? the origins of the ocellar nerves?

Fig. 5.—Vertical (longitudinal) section through one of the hemispheres, showing the origin of the commissural and antennal nerves and the optic lobe.

Fig. 6.—Longitudinal section through the brain and subœsophageal ganglion (× 50 diameters), showing the two portions of the calyx, the antennal lobe, and in the subœsophageal ganglion the three lobes giving off respectively the mandibular, maxillary, and labial nerves.

Fig. 7.—Longitudinal section through the optic ganglion and the eye; × 50 diameters.

Fig. 8.—Longitudinal section through the brain, showing the calyx, antennal lobes, and commissural lobes; × 50 diameters.

Fig. 8 *a*.—Enlarged view of Fig. 8 (× ⅛ B.), showing the relations in a longitudinal section of the calyx to the stalk, although the direct connection of the stalk with the calyx is not seen in this section.

PLATE XI.

Fig. 1.—Section 19 ($\times \frac{1}{2}$ A.), passing through the back of the brain, showing the posterior edge of the calices and antennal lobes and œsophageal commissural nerves and optic nerve. *tr.*, small tracheæ.

Fig. 2.—Section 20, passing through the back of the brain, showing the relation of the optic nerve to the optic ganglion and eye; the cornea, cones, rods, and retina of the eye are shown; $\times \frac{1}{2}$ A. *sup. n.*, superior, *m. n.*, median, and *inf. n.*, inferior commissural nerves connecting the hemispheres.

Fig. 3.—Enlarged view of upper part of the stalk and calyx, and the ganglion cells surrounding and filling the latter; $\times$ 225 diameters. 3 *a*, *b*, *c*, *d*, different ganglion cells seen from different directions, 3 *c* showing the large nucleus filled with coarse granules, but showing no nucleolus; one, however, is seen in Fig. 3 *b. ncl.*; $\times$ 725 diameters.

Fig. 4.—Longitudinal section of the brain and subœsophageal ganglion, magnified 50 diameters, showing the relations between the two, and of the origin of the œsophageal commissure from the upper side of each ganglion, *i. e.*, from the back of the brain and the upper side of the subœsophageal ganglion.

Fig. 5.—Enlarged view ($\times \frac{1}{2}$ B) of the subœsophageal ganglion of Fig. 6, Pl. X, showing the origin of the commissure to the first thoracic ganglion, and on the under side the three lobes (mandibular, maxillary, and labial), whence the nerves are sent to the mouth-appendages. *mand. l.*, mandibular lobe; *max. l.*, maxillary, and *max. l'.*, 2d maxillary or labial lobe; *com.*, commissure to subœsophageal ganglion.

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PLATE XII.

Fig. 1. Section No. 7 of brain of embryo *C. sorctus*, earliest stage observed, passing through the upper and lower cerebral (embryonic) lobes (*up. l.*, *low. l.*). (Do the upper cerebral lobes become the calices and the lower cerebral lobes ultimately become the trabeculæ?) (See fig. 8, *low. l.*). *op. l.*, optic lobe; *ant. l.*, antennal lobe; *eye*, outline of the eyes; × ½. Tolles's objective, A eye-piece.

Fig. 1*a*. Portion of the left upper cerebral lobe of fig. 1, magnified 400 diameters, showing the gradual passage of the cortical ganglion cells into the central granular nervous substance, the granules (*gran.*) extending and filling up the spaces between the nucleated ganglion cells (*gang. c.*); it will be noticed that there are at this time no nervous fibers.

Fig. 2. Section No. 5 of head of a more advanced embryo, just ready to hatch, the section not including any part of the brain, the cells represented being connective-tissue cells enveloping the brain. The portions left blank in figs. 1, 7, and 9 are in the actual sections filled with similar connective-tissue (mesodermic) cells.

Fig. 3. Section No. 6 of the same embryo, passing through the optic and antennal lobes.

Fig. 4. Section No. 7 of the same, passing through the "upper cerebral lobes" or calices of the future mushroom body (*cer. l.*), and also through the optic and antennal lobes.

Fig. 5. Section No. 8, passing through the brain (next behind No. 7).

Fig. 6. Section No. 9, passing through what is probably (?) the mushroom body marked as the cerebral lobe (*cer. l.*).

Fig. 7. Section No. 10. The parts not well defined.

Fig. 8. Section No. 11, through the brain of the same embryo as figs. 2-7, and passing through the upper and lower cerebral lobes, and the central body (*cent. b.*), at this point clearly indicated. Probably the "lower cerebral lobes" become the trabeculæ of the adult insect. The sections do not enable us to determine with exactitude the history of the embryonic upper and lower cerebral lobes. (For enlarged views of the upper and lower cerebral lobes and the central body see Plate xiii, fig. 4); *int.* indicates the integument of the head.

Fig. 9. Section No. 12 of the same embryo: *up. l.*, upper, *low. l.*, lower, cerebral lobes; *œs.*, œsophagus (compare also figs. 6 and 7 of Plate xiii, representing sections behind the head of the same embryo).

Fig. 10. Section No. 6 of the younger embryo, passing in front of No. 7, fig. 1, of this plate, and representing the subœsophageal ganglion, showing the form of the ganglion and the relation of the central granular nervous matter (*gran.*) to the envelope of cortical cells (*gang. c.*): × ½. Tolles's objective, B eye-piece.

Figs. 2-9 were drawn with the same objective, A eye-piece.

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PLATE XIII.

Fig. 1. Section through the brain of *Caloptenus bivittatus* in the third larval stage, showing the two hemispheres or sides of the brain and the ocelli and ocellar nerves, which are seen to arise from the top of the hemispheres directly over the calices (compare Plate ix, fig. —); *o. cal.*, outer calyx of left mushroom body. The lighter portions represent the granulo-fibrous central part of the brain, and the dark the cortical ganglionic cells; $\times \frac{1}{2}$ A.

Fig. 2. The right hemisphere of fig. 1 magnified 225 diameters, showing the mushroom body, its peduncle (*p.*), cauliculus (*cau.*), and outer (*o. cal.*) and inner (*i. cal.*) calices, and the bundles of fibers variously distributed to the optic and commissural lobes.

Fig. 3. Section passing immediately in front of that represented in fig. 1, and showing the calices without the stalk, and the œsophageal commissural lobe and its commissure (*com.*); the two hemispheres are united below; separate in fig. 1.

Fig. 4. Enlarged view ($\times$ 400 diameters) of the central body and contiguous parts from section 11 of the older embryo of *C. spretus*, represented in Plate xii, fig. 8, *cent. b.* and *low. l.* The central body is seen to be separated from the other parts by a partition of ganglion cells. Are the four ganglion cells in the upper part the rudimentary cellular bodies? Only the right half of the central body is drawn. The right half of the upper cerebral lobe is represented (*up. l.*), and below the entire trabecula, as it appears to be.

Fig. 5. Section No. 8 of the first thoracic ganglion of the youngest embryo (see, also, Plate xii, figs. 1, 1*a*, and fig. 10). The hour-glass-shaped ganglion consists of inner granular nervous matter (*gran.*), with no fibers present, and of a layer of cortical ganglionic cells (*gang. c.*), the layer being thickest on the under side of the ganglion and wanting at and near the middle of the upper side. Magnified 225 diameters.

Fig. 6. Section No. 15 of older embryo, represented also by figs. 2–9 of Plate xii, showing the nervous cord (*n. c.*), surrounded by connective-tissue cells; $\times \frac{1}{2}$ A.

Fig. 7. Section No. 16 through the same embryo, posterior to section 15, the cord being smaller than in section 15. These sections were cut just in front of the stomach and cœca.

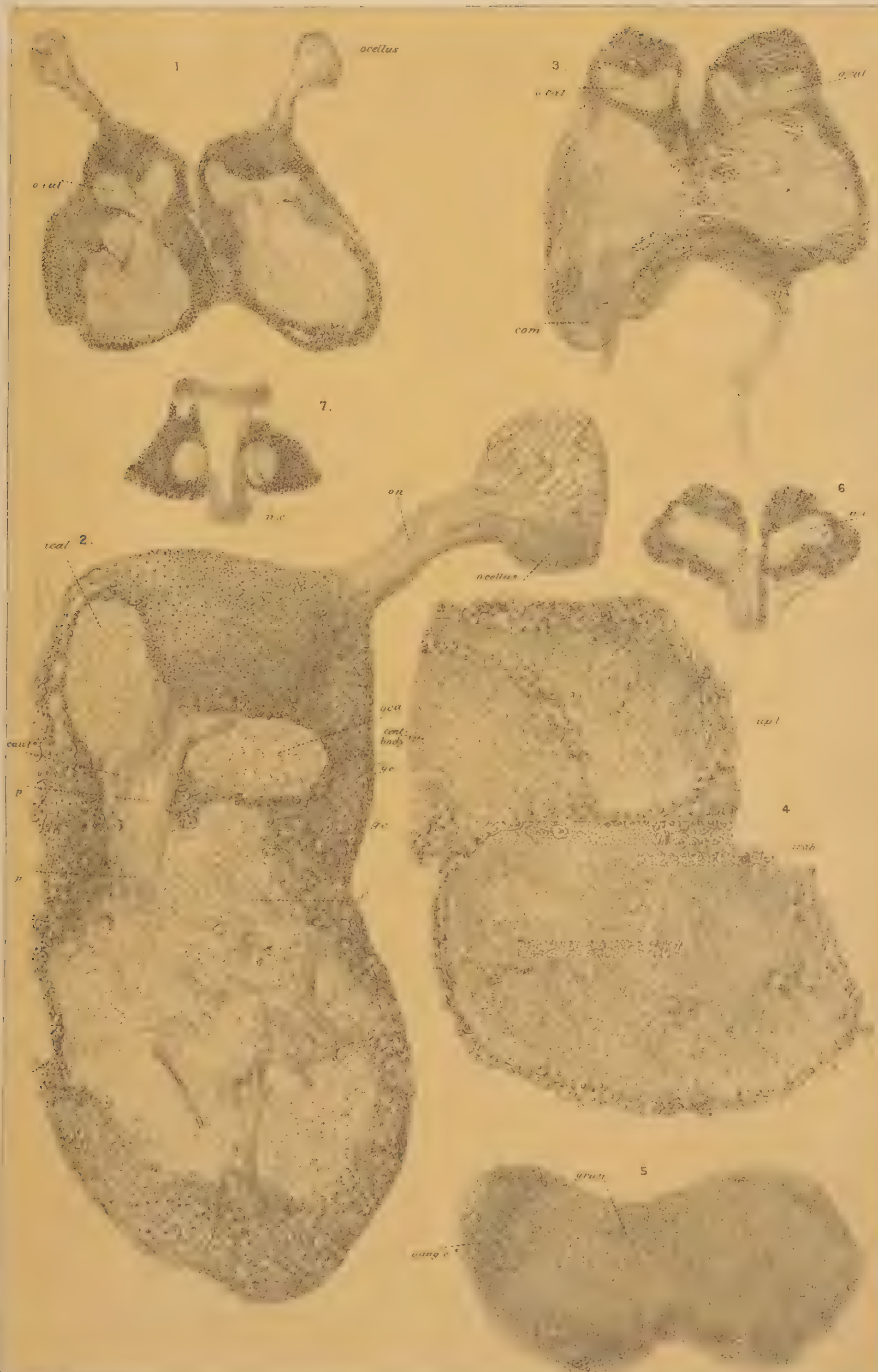

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PLATE XIV.

FIG. 1.—Enlarged view of brain and eye of *C. spretus* in the second pupal stage; × ½ A. This view of the brain is taken from the same preparation (No. 10) as Fig. 1, Plate XV. *Centr. b.*, the central body, showing the two series of cells in the lower division and the two rows of unicellular bodies in the superior division; *œ com. l.*, œsophageal commissural lobes, with the ball-like masses distinctly seen, though this preparation was stained only with picrocarmine, *œ. com.*, œsophageal commissure; *opt. nrl.*, optic nervules; *retina*, retina with rods and cones beyond, the cornea not shown.

FIG. 2.—The central body of adult *C. spretus*, from section 17, showing the inferior and superior divisions, the cells in inferior division (*inf.*) and the two rows of unicellular bodies (*uc. cell. b.*) in the superior division (*sup*). Magnified 225 diameters.

FIG. 3.—The central body of the second or last pupal state, from section No. 10; *c*, cells in the fibrous septum between the lower and upper divisions of the central body, from section No. 11. × 225 diameters.

FIG. 4.—Vertical section of the subœsophageal ganglion of the cockroach (*Blatta orientalis*), showing the commissure on the left side.

FIG. 5.—A section farther behind, showing the back of the ganglion (*gang.*), seen separate from the commissure (*com*).

FIG. 6.—A section through the commissure just behind the ganglion.

All the sections represented on this plate were stained with picrocarmine.

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THE BRAIN OF THE LOCUST

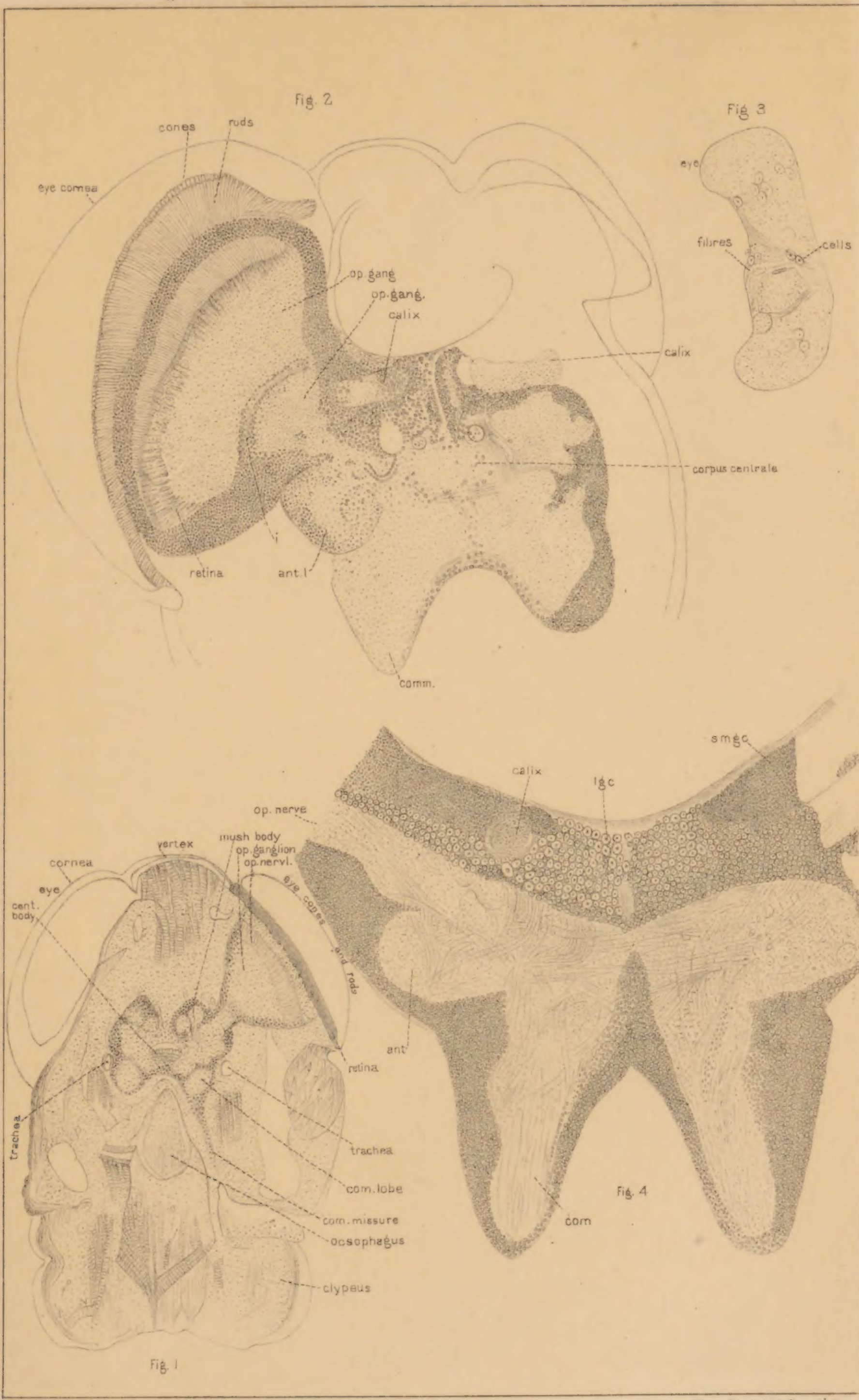
PLATE XV.

FIG. 1.—Frontal section No. 10, through the head of second or last pupal stage of *C. spretus*, passing through the middle of the brain, the optic ganglion, and eyes, and cutting across the œsophagus. Drawn in order to show the relation of the brain to the eyes and the exterior of the head ; magnified 30 diameters. In the brain the right mushroom body is seen, while the optic and antennal lobés are not so well marked. The central body (*centr. b.*) is cut through near the middle; below are the trabeculæ (*trab.*), next to the commissural lobes, two tracheæ (*tr.*) or air-tubes passing near the brain. The commissure to the subœsophageal ganglion is drawn on the right side, passing down the œsophagus. In the eye the cornea, the respective portions composed of rods and cones, the black retina, the stratum of optic nervules, and the optic ganglion and optic nerve passing off from the optic lobe are all well marked.

FIG. 2.—Section through the brain and eyes of the same second pupa of *C. spretus*, passing through the anterior part of the calices, but not through the central body. The section is oblique and does not well represent the right side.

FIG. 3.—Calyx of the section represented by Fig. 2; magnified 225 diameters. It is composed of granulated nerve substance with a few fibers, the continuation of those of the stalk, and with a few ganglion cells.

FIG. 4.—Section through the back of brain of the adult *Locusta Carolina*, passing behind the mushroom body, showing the œsophageal commissures, the antennal lobes, and the bundle of nerve-fibers crossing to the right hemisphere. The left calyx is cut through, the microtome-razor passing behind and not grazing the right mushroom body. The distribution of the large (*l. g. c.*) and small ganglion cells (*sm. g. c.*) is well seen in this section. It will be seen that the brain of *Locusta Carolina* does not differ in any respect from that of *Caloptenus spretus*, so far as the sections show.



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THE BRAIN OF THE LOCUST.